

The socially parasitic ant genus *Strongylognathus* Mayr in North Africa (Insecta: Hymenoptera: Formicidae)

MATTHIAS SANETRA¹ & ROBERT GÜSTEN²

Institut für Zoologie, Technische Universität Darmstadt, Schnittspahnstr. 3, D-64287 Darmstadt, Germany
Present addresses:

¹ *School of Tropical Biology, Department of Zoology & Tropical Ecology, James Cook University, Townsville 4811, Queensland, Australia; e-mail: matthias.sanetra@jcu.edu.au*

² *Hessisches Landesmuseum Darmstadt, Zoologische Abteilung, Friedensplatz 1, D-64287 Darmstadt, Germany; e-mail: guesten@hlmd.de (corresponding author)*

Abstract

Morphological examination of *Strongylognathus* specimens from 14 of 15 known sites in Tunisia, Algeria and Morocco revealed that only one species occurs in that part of the Palaearctic region. *S. foreli* Emery, 1922 falls into synonymy with *S. afer* Emery, 1884. Redescriptions of all morphs and allozyme data are provided. Four new records of *S. afer* are presented from Tunisia which extend the known range in this country to more southerly regions and allow some conclusions on ecological requirements. Observations of slave raids in the laboratory showed that *S. afer* is a dulotic social parasite using *Tetramorium semilaeve* André, 1883 as its host. Taxonomy, distribution and life history are discussed with respect to related species of the Mediterranean region.

Key words: Myrmicinae, Tetramoriini, *Strongylognathus afer*, social parasitism, ecology, distribution, allozymes

Introduction

Strongylognathus Mayr, 1853 is a widespread Palaearctic ant genus, which exclusively comprises permanent social parasites dependent on *Tetramorium* Mayr, 1855 host species. Despite being well represented in Europe and Asia (e.g., Pisarski 1966, Baroni Urbani 1969, Radchenko 1991), taxonomy and distribution of most *Strongylognathus* species still remain unsatisfactorily known. Bolton (1976), when diagnosing *Strongylognathus* and the tribe Tetramoriini (Myrmicinae), has pointed out that many of the species level names in *Strongylognathus* may merely represent local populations and, with more information becoming available, the number of valid species will dwindle considerably. The compre-

hensive list of Bolton (1995) recognizes 26 species, not taking into account the synonymy of *S. ruzskyi* Emery, 1909 with *S. christophi* Emery, 1889 proposed by Radchenko (1991). Two synonyms of *S. destefanii* Emery, 1915 (*S. cecconii* Emery, 1916 and *S. emeryi* Menozzi, 1921) have since then been established (Sanetra *et al.* 1999), bringing the number of taxa currently residing in species rank to 23.

Two nominal species of *Strongylognathus* have been described from northern Africa. *S. afer* was based on a single female from Dhaya in the Atlas mountains of western Algeria (Emery 1884). Emery (1909) then erected "*Strongylognathus huberi huberi* var. *foreli*" from Algeria, made available by Emery (1922) as *S. huberi* ssp. *foreli* and provisionally raised to species level by Bolton (1976). The worker syntypes were part of collections made by Forel (1890a, 1890b) at three localities in the northeastern part of Algeria (Souk-Ahras, Duvivier) and northern Tunisia (Béja). Forel also mentions a previous Tunisian finding, which we could not track down in the literature.

After a long lapse of time, *S. afer* was re-recorded from Algeria by Cagniant (1970) and cited for the first time from Morocco by Cagniant (1997). No findings from Tunisia were ever added to Forel's (1890a, 1890b) locality Béja, although we have discovered specimens in public collections originating from two or three samples taken early last century near Le Kef, variously determined as either *S. afer* or *S. foreli*. In the present study, the synonymy of *S. foreli* with *S. afer* is established, the species is redescribed, and four new records from Tunisia as well as the first life history information are presented.

Material and Methods

Material investigated

The new material from Tunisia was collected by one of us (MS) during a research trip in 1997 and by A. Schulz & K. Vock (Leichlingen, Germany) in 1995. Reference samples are deposited in MCSN, MHNG, NHMB, the senior author's collection, coll. A. Schulz, CXE, CHC, CAT and coll. S. Schembri (Zebbug, Malta). Further specimens from the following collections have been studied:

MCSN (Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy)

MHNG (Muséum d'Histoire Naturelle de Genève, Switzerland)

NHMB (Naturhistorisches Museum Basel, Switzerland)

IEGG (Istituto di Entomologia "Guido Grandi" de l'Università, Bologna, Italy)

ZMHB (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany)

CXE (collection of X. Espadaler, Barcelona, Spain)

CHC (collection of H. Cagniant, Toulouse, France)

CAT (collection of A. Tinaut, Granada, Spain)

Measurements

Measurements were taken using a stereo microscope Wild M 400 at a magnification of 100x equipped with an ocular micrometer, to the nearest 0.01mm. Recent taxonomic works on *Strongylognathus* differ widely in the measurements and indices employed (compare, e.g., Baroni Urbani 1969, Radchenko 1991). For workers and females, we provide here the following standard measurements and indices: ML (mesosoma length); HW (head width); HL (head length); SL (scape length); PW (petiolus width); PPW (postpetiolus width); CI (cephalic index: HW/HL); SI (scape index: SL/HL); PI (petiolar index: PW/PPW).

Only ML was determined for males. Data are given as mean±standard deviation(range), to the nearest 0.005mm for measurements and 0.005 for indices. A few tiny workers, which additionally showed malformations, were excluded.

We are sceptical about the taxonomic value of several further measurements and indices given by Baroni Urbani (1969), yet some of these may deserve scrutiny in future revisions. Unfortunately, some authors differ in definitions of those measurements used in common. We follow Seifert (1996) and Baroni Urbani (1969) in general. To preserve comparability with the latter, HW was measured behind (instead of including) the eyes despite a loss in accuracy. HL is given to the mid of the occipital margin and not to an imagined line between occipital corners as did Radchenko (1991) because this introduces unnecessary imprecision. ML in workers was measured from the propodeal lobes to the point where the convex pronotal declivity meets the concavity towards the anterior rim, and not to the "place of connection with head" (Radchenko 1991), a specification unclear to us.

Electrophoresis

Allozyme electrophoresis was carried out on parasites and hosts from the collected *Strongylognathus* colonies as well as on non-parasitized *Tetramorium* colonies obtained during the 1997 collection trip, using the methods described in Sanetra *et al.* (1994) and Sanetra and Buschinger (2000). Sanetra *et al.* (1994, 1999) have shown that this biochemical method is able to yield valuable characters for species delimitation and recognition in Palearctic *Tetramorium*, which is very difficult on a purely morphological basis. The usefulness of allozyme data in *Strongylognathus*, however, is limited. The following loci were chosen here: glucose-6-phosphate isomerase [*Gpi*, EC 5.3.1.9], glycerol-3-phosphate dehydrogenase [*G3pdh*, EC 1.1.1.8], isocitrate dehydrogenase [*Idh*, EC 1.1.1.14], malate dehydrogenase [*Mdh-1*, EC 1.1.1.37], phosphoglucosmutase [*Pgm*, EC 5.4.2.2] and pyruvate kinase [*Pk*, EC 2.7.3.3].

Slave raids

Tetramorium colonies both pure and infested by *S. afer* were temporarily kept in the laboratory in small plastic boxes containing a thin layer of plaster. For each colony, one box was filled with moistened tissue paper as a nest chamber, while a second one connected by flexible rubber hose served as a foraging arena. For ethological experiments to

detect and observe slave raiding behavior by *S. afer*, a parasite colony and a potential host colony were placed in different parts of a divided arena (100 x 40 cm) with a plaster surface. Opening of a passage-way between the two parts allowed the slave-makers to start a raid.

Results

Taxonomy and redescription

The holotype of *Strongylognathus afer* from western Algeria (Dhaya), a dealate female deposited in MCSN, was compared with the other North African *Strongylognathus* females available, all collected in Tunisia (Makthar, J. Gora'a, Nefza, Le Kef; see listing of material below). All these were morphologically virtually identical (see redescription below). The female sexuals however, were unknown for var. *foreli* when Emery (1909) first described it. A comparison of the 8 worker samples now known from eastern Algeria and Tunisia provided convincing evidence for the conspecificity of all these populations, thus allowing the assignment of the Tunisian females to *S. foreli*. In addition to the virtual identity of females from that region with the *S. afer* holotype, investigation of workers from central Algeria and Morocco also revealed no differences of taxonomic significance from the Tunisian material. Consequently, *S. foreli* Emery, 1922 sinks into synonymy with *S. afer* Emery, 1884.

Forel's material from his 1889 North Africa excursion (reported in detail in Forel 1890b) originally included *Strongylognathus* workers from one Tunisian and two Algerian localities. Nevertheless, when Emery (1909) described var. *foreli* based on material received from Forel, he mentioned only „Algeria“ as the type locality. Indeed, all 21 specimens in Emery's collection at MCSN bear the locality indication „Duvivier“. Thus, the restricted type locality of *S. foreli* Emery, 1922 is Bouchegouf (formerly Duvivier) in the Seybousse Valley, Wil. Annaba, Algeria.

Strongylognathus afer Emery, 1884

Strongylognathus huberi huberi var. *foreli* Emery, 1909 (name unavailable)

Strongylognathus huberi ssp. *foreli* Emery, 1922: **syn. nov.**

Strongylognathus foreli Emery: Bolton 1976

Collecting data: **Tunisia** - Gouv. Siliana, road Makthar-Tebessa, 6 rkm W Makthar, ca. 900m, X.1995, leg. A. Schulz & K. Vock: dealated ♀ crawling on the ground; Gouv. Siliana, Forêt de Kesra, ca. 7 rkm N Kesra, ca. 1000m, 05.IV.1997, leg. M. Sanetra: numerous ♂♂ in a nest of *Tetramorium semilaeve*; Gouv. Béja, Mts de Tébourouk, Jebel Gora'a, ca. 800m, 04.IV.1997, leg. M. Sanetra: numerous ♂♂ and queen in a nest of *T. semilaeve*; Gouv. Béja, ca. 6 rkm S Nefza, Jebel Sidi Ahmed, ca. 300m, 11.IV.1997, leg. M. Sanetra: numerous ♂♂ and queen in a nest of *T. semilaeve*.

Other investigated material: **Tunisia** - 8♀♀, 4♀♀, 10♂♂: Le Kef [650m], 1909/10, leg. Dr. Normand (NHMB: 8♀♀, 4♀♀, 9♂♂, MCSN: 1♂; unpubl.); 1 ♀, 1 ♂: Le Kef, „Dr. Santschi“ [leg. ?] (NHMB; unpubl.); 27♀♀: Dir el Kef, 900m, 22.V.1913, leg. F. Santschi [?] (NHMB: 26♀♀, IEGG: 1♀; unpubl.); 22♀♀: Béja [250m], IV.1889, leg. A. Forel (MHNG: 11♀♀, NHMB: 4♀♀, IEGG: 1 ♀, ZMHB: 6♀♀; Forel 1890a, 1890b); **Algeria** - 12♀♀: mt. near Souk-Ahras, close to summit, ca. 1500m [probably erroneous], IV.1889, leg. A. Forel (MHNG; Forel 1890a, 1890b); 29♀♀: Duvivier [now Bouchegouf, 300m], IV.1889, leg. A. Forel (MHNG: 6♀♀, MCSN: 21♀♀ syntypes of *Strongylognathus huberi* ssp. *foreli* Emery, IEGG: 2♀♀; Forel 1890a, 1890b); 13♀♀: Massif de l'Ouarsenis, Teniet-el-Haad, 1500m, 10.V.1968, leg. H. Cagniant (CXE; Cagniant 1970); 1 ♀ holotype of *Strongylognathus afer* Emery: Dhaya [1350m], leg. Bedel (MCSN; Emery 1884); 1♀: Saharian Atlas, Ain Aïssa ravine, 1350m, 07.VI.1968, leg. H. Cagniant (CHC; Cagniant 1970); **Morocco** - 8♀♀: High Atlas, Tizgui near Amez Miz, 1300m, 09.V.1983, leg. H. Cagniant & X. Espadaler (CXE: 7♀♀, CHC: 1♀; Cagniant 1997); 2♀♀: Rif mts., around Ras el Ma (near Chefchaouen), 16.IV.1984, leg. A. Tinaut (CAT; unpubl.); **no locality label** - 3♀♀: probably Béja, IV.1889, leg. A. Forel (NHMB); 1♀: probably Duvivier, IV.1889, leg. A. Forel (IEGG)

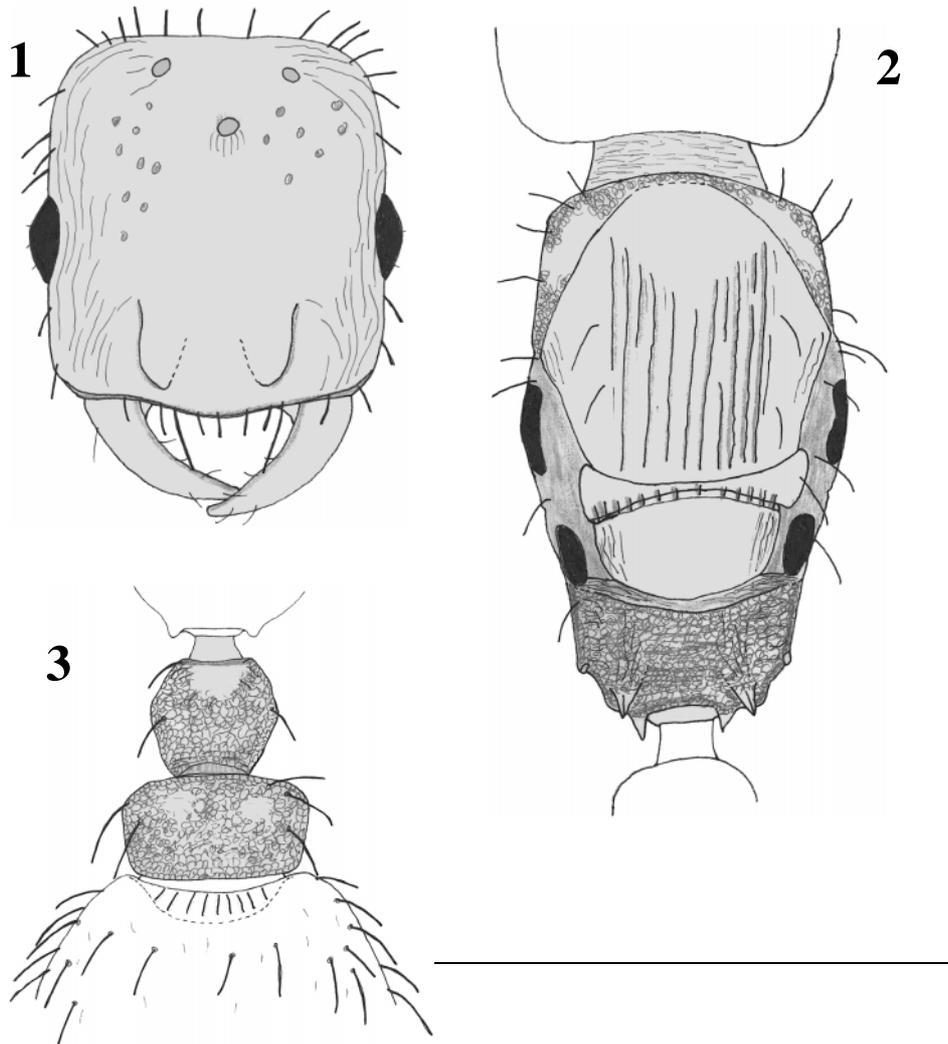
Further record (no material seen): **Algeria** - Massif de l'Ouarsenis, Jebel Berrouaghia, 850m, 27.III.1967, leg. H. Cagniant (Cagniant 1970)

Female

Measurements and indices (n=9): ML 1.105 ± 0.035 (1.070-1.180)mm, HW 0.630 ± 0.015 (0.620-0.660)mm, HL 0.740 ± 0.015 (0.720-0.760)mm, SL 0.485 ± 0.020 (0.470-0.530)mm, PW 0.250 ± 0.015 (0.230-0.280)mm, PPW 0.380 ± 0.020 (0.350-0.430)mm, CI 0.855 ± 0.010 (0.840-0.870), SI 0.660 ± 0.020 (0.625-0.695), PI 0.660 ± 0.030 (0.615-0.711)

Notably smaller than other species of the *S. huberi* group except *S. caeciliae* Forel, 1897 and *S. minutus* Radchenko, 1991. Head considerably smaller than in worker, mesosoma only slightly longer; female/worker thorax volume ratio (see Stille 1996) 2.1-2.2 as measured for samples from Nefza, J. Gora'a and Le Kef. Head nearly as wide as long, widest at eye level or somewhat posteriorly (eyes excluded) but lateral margin only very slightly convex (Fig. 1). Occipital corners rather rounded and posterior margin weakly concave. Scape when directed backwards fails to reach occipital margin by about 1½ times its greatest width. Eyes situated medially on head sides, somewhat bulging (greatest diameter 0.180-0.190mm). Head surface generally smooth and shining medially, almost without any sculpture in some specimens but shallow longitudinally striate over most of the surface in others. Lateral parts always longitudinally rugose with some anastomosing, posteriorly converging archedly to lateral ocelli. Pronotal corners rather angular, well visible from above. Propodeal teeth developed as short acute denticles, sometimes nearly absent. Mesoscutum with distinct longitudinal rugosity and weak microsculpture except for anterior central and posterior lateral portions, which are smooth and shiny, as are scutellum and metanotum except on their outermost parts (Fig. 2). Propodeum and often also lateral parts of mesosoma with well developed punctate-reticulate microsculpture and some

rugae, especially around the pronotal corners. Petiolar nodes as in Fig. 3, surface largely covered with distinct microsculpture as on propodeum, weak to absent only around center of petiolus; rugosity scarce and indistinct if present at all. Body color dark blackish brown in fresh specimens, first gastral tergite and especially appendages lighter.

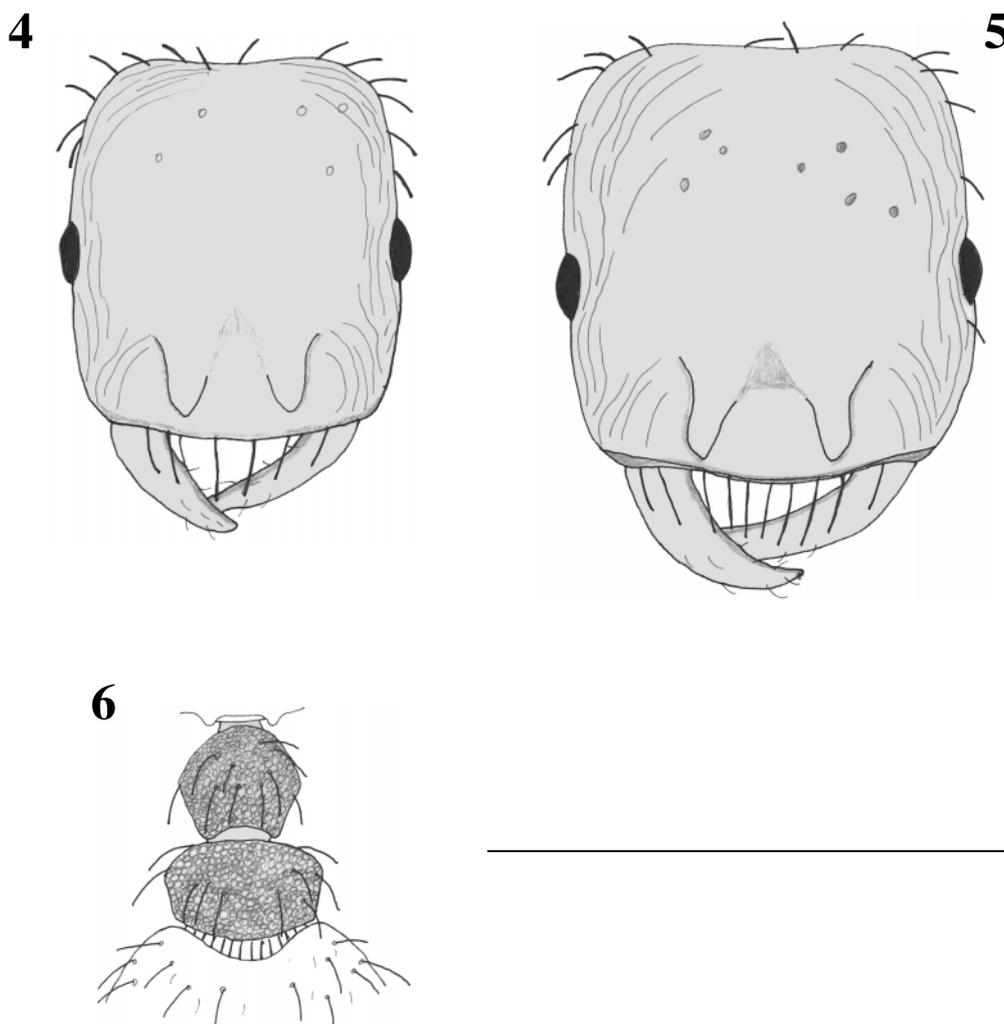


FIGURES 1-3. *Strongylognathus afer* Emery, female (queen) from J. Gora'a. 1, Head (frontal view); 2, mesosoma (dorsal view); 3, petiolar nodes (dorsal view); scale bar 1mm; drawings by A. Schulz.

Variability: The nine specimens differ to some extent in sculpturing of the central head and lateral mesosoma surfaces, but are in general very similar to each other. The queen from Nefza, the only known female sexual from a lowland site, is considerably larger than the other specimens.

Worker

Measurements and indices (n=109): ML $0.950\pm 0.050(0.830-1.050)$ mm, HW $0.695\pm 0.035(0.590-0.770)$ mm, HL $0.795\pm 0.035(0.670-0.860)$ mm, SL $0.530\pm 0.025(0.460-0.580)$ mm, PW $0.225\pm 0.015(0.190-0.260)$ mm, PPW $0.295\pm 0.020(0.260-0.330)$ mm, CI $0.875\pm 0.015(0.840-0.940)$, SI $0.665\pm 0.015(0.635-0.700)$, PI $0.765\pm 0.025(0.705-0.815)$. Data apportioned to the separate samples are itemized in Table 1 (range not given).



FIGURES 4-6. *Strongylognathus afer* Emery, workers. 4, Head (frontal view) of worker from J. Gora'a (smallest specimen); 5, head (frontal view) of worker from Nefza (largest specimen); 6, petiolar nodes (dorsal view) of worker from Nefza (same as 5); scale bar 1mm; drawings by A. Schulz.

TABLE 1. Measurements and indices for workers of *Strongylognathus afer* Emery from different localities. n: number of specimens studied; ML: mesosoma length; HW: head width; HL: head length; SL: scape length; PW: petiolus width; PPW: postpetiolus width; CI: cephalic index: HW/HL; SI: scape index: SL/HL; PI: petiolar index: PW/PPW. All data given as mean±standard deviation.

Locality	n	ML (mm)	HW (mm)	HL (mm)	SL (mm)	PW (mm)	PPW (mm)	CI	SI	PI
nr Makthar					no ♂♂ collected					
Forêt de Kesra	10	0.925 ±0.035	0.675 ±0.025	0.770 ±0.025	0.520 ±0.020	0.220 ±0.015	0.285 ±0.020	0.875 ±0.010	0.670 ±0.010	0.775 ±0.025
J. Gora'a	15	0.935 ±0.065	0.675 ±0.045	0.780 ±0.050	0.515 ±0.025	0.220 ±0.015	0.290 ±0.015	0.865 ±0.010	0.660 ±0.015	0.755 ±0.030
nr Nefza	5	0.970 ±0.045	0.710 ±0.030	0.810 ±0.035	0.540 ±0.015	0.235 ±0.015	0.305 ±0.015	0.875 ±0.020	0.670 ±0.020	0.775 ±0.025
Le Kef	7	0.995 ±0.035	0.715 ±0.055	0.800 ±0.060	0.550 ±0.040	0.235 ±0.010	0.310 ±0.015	0.895 ±0.020	0.690 ±0.010	0.760 ±0.010
Dir el Kef	13	0.980 ±0.030	0.725 ±0.015	0.815 ±0.010	0.550 ±0.010	0.240 ±0.010	0.310 ±0.010	0.890 ±0.015	0.675 ±0.010	0.765 ±0.025
Béja	14	0.980 ±0.035	0.720 ±0.025	0.820 ±0.025	0.545 ±0.015	0.235 ±0.015	0.305 ±0.015	0.880 ±0.010	0.665 ±0.010	0.765 ±0.025
nr Souk-Ahras	12	0.925 ±0.035	0.665 ±0.035	0.765 ±0.030	0.510 ±0.025	0.215 ±0.010	0.280 ±0.010	0.870 ±0.015	0.665 ±0.010	0.760 ±0.020
Boucheouf	10	0.945 ±0.035	0.695 ±0.020	0.790 ±0.020	0.515 ±0.015	0.235 ±0.010	0.305 ±0.010	0.880 ±0.010	0.650 ±0.010	0.760 ±0.030
J. Berrouaghia					not investigated					
Teniet-el-Haad	13	0.905 ±0.020	0.675 ±0.015	0.775 ±0.020	0.515 ±0.015	0.205 ±0.010	0.270 ±0.010	0.870 ±0.010	0.665 ±0.015	0.760 ±0.025
Dhaya					no ♂♂ collected					
Aïn Aïssa	1	0.990	0.710	0.830	0.550	0.240	0.310	0.855	0.665	0.775
Tizgui	8	0.980 ±0.055	0.710 ±0.040	0.810 ±0.035	0.540 ±0.030	0.230 ±0.020	0.300 ±0.020	0.885 ±0.020	0.665 ±0.020	0.765 ±0.025
Ras el Ma	1	0.970	0.730	0.830	0.530	0.220	0.290	0.880	0.640	0.760
All	109	0.950 ±0.050	0.695 ±0.035	0.795 ±0.035	0.530 ±0.025	0.225 ±0.015	0.295 ±0.020	0.875 ±0.015	0.665 ±0.015	0.765 ±0.025

Smaller than other species of the *S. huberi* group except *S. minutus*. Head scarcely longer than wide, widest at eye level (eyes excluded), in few specimens somewhat behind the eyes. Head sides variable, generally more convex than in females (Figs 4, 5). Occipital margin weakly concave. Convexity of head sides and concavity of occipital margin slightly more distinct in large examples, resulting in an allometric increase of CI with body size (see Tab. 1). Scape when directed backwards fails to reach occipital margin by about 1½ times its greatest diameter. Eyes situated medially on head sides, smaller than in females (greatest diameter 0.120-0.130mm) and bulging only very little, decidedly less so than e.g. in *S. huberi* workers (compare to Fig. 20 in Sanetra *et al.* 1999). Head surface sculpture very restricted, lateral parts showing shallow longitudinal striation to a variable

extent, posteriorly curving slightly towards center but then disappearing. Some individuals with few very weak short striae on center of head capsule. Pronotal corners can be rather angular, but smoothly rounded in other specimens. Propodeal teeth extremely variable from virtually absent to (rarely) rather distinct upright denticles. Lateral surfaces of mesosoma with variably developed irregular longitudinal rugosity, dorsal surface except propodeum completely smooth and shiny in most specimens but with punctate-reticulate microsculpture throughout and hints of longitudinal rugae in some. Petiolar nodes as in Fig. 6, surface appearing shiny but completely covered with shallow but dense microsculpture, with a pair of weak rugae laterally on postpetiolus or none at all. Body color varying from uniformly light yellowish-brown to yellowish-brown with darker centres of heads, sometimes body ochrish-brown and heads wholly dark brown.

Variability: The worker caste generally exhibits much more intra- and intercolonial variation in body size (see Tab. 1), head shape, surface sculpture and color than the investigated sexuals. At the lower altitude sites, specimens have been found to be comparatively large (Nefza, Béja) to medium-sized (Bouchegouf), lightly and uniformly colored, with the head sides relatively distinctly convex much as in *S. destefanii* (Fig. 5, compare to Fig. 21 in Sanetra *et al.* 1999). Two samples from around Le Kef are much like the one from Béja. Workers taken on J. Gora'a are darker and distinctly smaller on average, but show extreme size variation. Their heads usually display an entirely dark brown coloration contrasting with other body parts, and – mainly in small individuals – less distinctly convex sides (Fig. 4), thus superficially resembling *S. alpinus* Wheeler, 1909. Those from higher up in the Forêt de Kesra (which those from Souk-Ahras most strongly resemble) show heads not quite as dark and lighter on the sides than in the center, but color variability is very marked, some individuals being wholly yellowish-brown as at Nefza. However, Kesra workers are uniformly small in size. Unlike the other mountainous sites, the Algerian Teniet-el-Haad harbored the most lightly colored workers. Also, they are the smallest and very uniform. Some of the largest workers originate from the Moroccan High Atlas, having a slender appearance faintly recalling *S. huberi* because of the narrowish mesosoma and in some instances a narrow head, but head shape as well as overall size are highly variable in this sample. Specimens from the Rif mountains show no noteworthy features. The single worker from the Saharian Atlas has the occipital corners more rounded than any other individual and shows some additional rugae on the postpetiolus but is otherwise much like specimens from northern Tunisia. As regards variability in surface sculpture, intranidal variation appears to be more distinct than that among colonies or populations. Variation in propodeal spine development can even be intraindividual, as the left and right side differ considerably in some specimens.

Male

Mesosoma length (n=10): ML 1.570 ± 0.055 (1.500-1.660)mm

Known only from two probably separate samples from Le Kef, Tunisia. Similar to female in size. Head slightly elongate with strong punctate-reticulate sculpture throughout.

Mesosoma with fine longitudinal rugosity above a microsculpture mainly along sutures, otherwise smooth and shining. Propodeum and petiolar nodes bearing strong punctate-reticulate sculpture, propodeal teeth similarly variable as in females. Male genitalia have not been examined as yet, owing to the very limited number of specimens and the undetermined taxonomic value of this character in the tribe Tetramoriini.

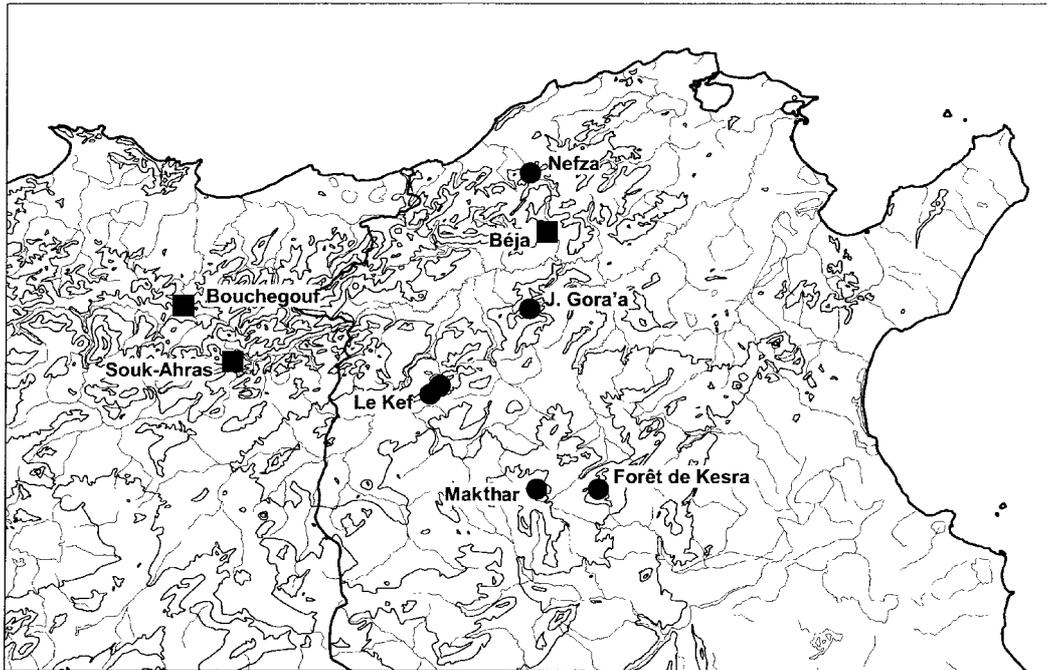


FIGURE 7. Distribution of *Strongylognathus afer* Emery in northern Tunisia and northeastern Algeria. Squares: literature data; circles: new records. The location of Dir el Kef could not be ascertained, presumably this denomination refers to a mountainous site near Le Kef.

Distribution and habitat specifications

The presented maps (Figs 7, 8) show the hitherto known distribution of *Strongylognathus afer* in northern Africa. Although the information available is still rather scanty, the nine recorded localities (six of them newly published here) from eastern Algeria and Tunisia (Fig. 7) indicate that the species inhabits a wide variety of climatically and ecologically different sites. Only one locality in each country is situated on the northern slope of the coastal mountain range, where a true mediterranean-humid climate with a mean annual precipitation (m.a.p.) of at least 1000mm prevails. On the leeward side of the coastal mountain chain, Béja still exhibits a moderately humid climate (m.a.p. 630mm). Along the coastal ranges, natural climax vegetation would be olive-pistachio forest (*Olea-Lentiscetum*) on the north slope and mediterranean oak forest on the southern side, but today only remnants have survived in limited areas. Due to the intense exploitation as agricultural and

grazing land, the search for *Strongylognathus* in the coastal range proved challenging, and certainly the distribution of the species in that region is much more fragmented today than it was in former times. The colony discovered near Nefza had established its nest site at the margin of a small olive orchard, and in the surroundings, shrub vegetation mainly composed of *Genista* was predominant.

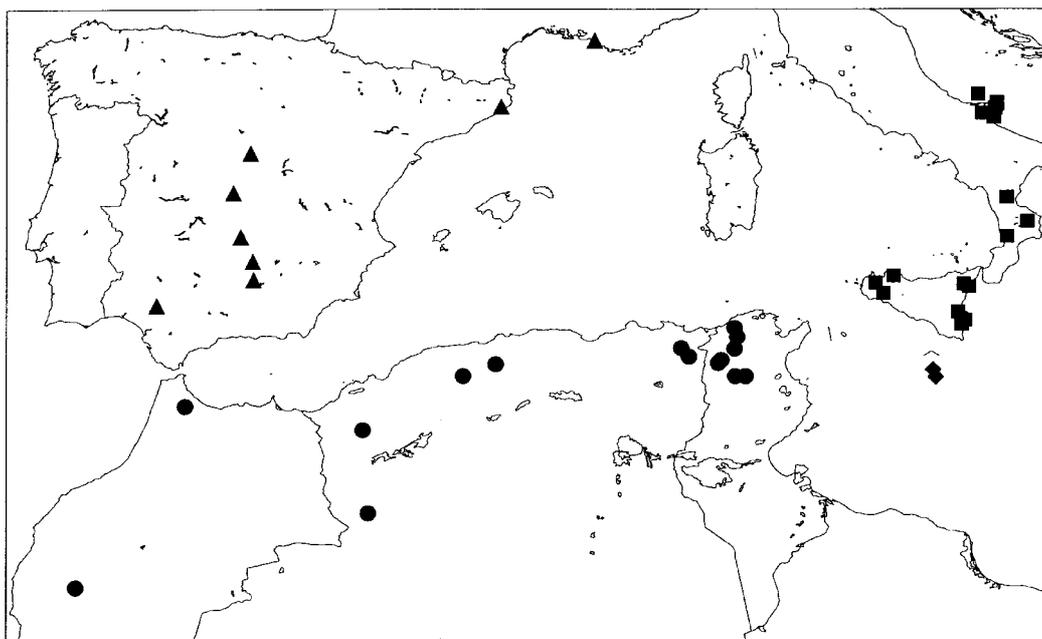


FIGURE 8. Distribution of *Strongylognathus* species in the western Mediterranean. Circles: *S. afer* Emery; Triangles: *S. caeciliae*¹ Forel; Squares: *S. destefanii* Emery; Diamonds: *S. insularis* Baroni Urbani.

In contrast to the above-mentioned sites, regions farther inland in Tunisia, such as the Medjerda valley and the so-called High Tell are to be included in the mediterranean-semi-arid bioclimate zone roughly delimited by the 600mm isohyet (Gießner 1984). The *S. afer* records from the latter area (see Fig. 7) stem from heights of 800-1000m in prominent mountain ranges with somewhat higher humidity as well as lower winter temperatures. The single discovery in the corresponding part of Algeria (Forel 1890b) was made even higher up (though Forel's specification of 1500m seems incorrect as peaks around Souk-Ahras do not exceed 1250m). Mean annual precipitation near the mountainous collecting sites ranges from 510mm (Le Kef) to 730mm (Souk-Ahras). Aleppo pine associations combined with maquis containing holm oak and juniper would be naturally occurring there, rarely also true oak forests in the most humid situations (Gießner 1984). However,

1. Published localities only. One record from Marseille (Emery 1909), hitherto referred to *S. huberi*, is here tentatively allocated to *S. caeciliae* after investigation of a ♀ in IEGG

the natural plant cover has been strongly degraded in many places by human influence. This applies in particular to the locality near Makthar, situated amidst grassy hillsides with limestone rocks heavily grazed by sheep and goats. In the nearby Forêt de Kesra, a colony of *S. afer* was found on a southwest facing slope in a deforested area used by livestock. In the Mts de Téboursouk near the radio tower on J. Gora'a some grazing occurred also.

Two of the colonies reported by Cagniant (1970) were found in the central Algerian Massif de l'Ouarsenis at elevations above 800m. This part of the Atlas mountains is separated from the coastal range by the Chéelif valley and immediately borders to the arid steppe zone in the south. Climatic conditions may be expected to resemble those in the Tunisian High Tell at the two localities close to Makthar (m.a.p. at Teniet-el-Haad 630mm). Cagniant (1970) reported a holm oak maquis with juniper at 850m and a shrubby clearing in cedar-dominated wood at 1500m. In the westernmost Algerian mountains, with the type locality of *S. afer* (Dhaya), generally drier conditions prevail and only the highest peaks may be comparable ecologically to the Massif de l'Ouarsenis. Surprisingly, another record has been obtained at this longitude even much farther to the south in the Saharian Atlas, beyond the very arid Hauts Plateaux. Particular environmental conditions evidently supported here, at least at the time of collecting, an open holm oak stand with juniper and olive trees in a steep-sided valley with permanent running water (Cagniant in litt.), even though at only slightly lower elevation at Ain Sefra semi-desert conditions prevail (m.a.p. below 200mm).

According to Cagniant (in litt.), *S. afer* was recorded in the Moroccan High Atlas at 1300m on a meadow with *Asphodilus* sp. and *Cistus* sp. along a creek, bordering an oak wood. No habitat information was available for the locality in the Rif mountains.

Allozyme variation

In view of the largely unresolved systematics of Palaearctic taxa in the genus *Tetramorium* and the difficulties of species delimitation through worker morphology, a preliminary survey of the Tunisian *Tetramorium* fauna by allozyme electrophoresis was undertaken. Contrasting electromorphs at the *Gpi*, *Idh* and *Pk* loci yielded the recognition of two clearly distinct species or species groups (Tab. 2). Comparison with collection material identified these as *T. semilaeve* André, 1883 and *T. biskrense* Forel, 1904, corroborated also by electrophoretic data from elsewhere (Sanetra *et al.* 1999, Sanetra & Buschinger 2000, note that terminology of electromorphs is different in the latter paper). Interestingly, 18 of 21 colonies of *T. semilaeve* were monomorphic at all loci studied (*T. semilaeve* (s.l.) from other parts of the Mediterranean region are more variable), while enzyme polymorphism was high in *T. biskrense*. The two entities are also distinguishable by the morphology of sexuals and, though only subtly and often not convincingly, by different sculpture of the workers.

As elaborated in Sanetra *et al.* (1994, 1999), allozyme electrophoresis is not a valuable tool to distinguish species in the genus *Strongylognathus*. The three investigated colonies

of *S. afer* did not differ from the usual pattern previously observed in other species of the *S. huberi* group at the studied loci. At the *Gpi* locus, only one allele common to all investigated species was found (Tab. 2), whereas a second one was also present among six colonies of *S. destefanii* from southern Italy studied in Sanetra *et al.* (1999).

TABLE 2. Allozyme electrophoretic results for *Tetramorium* and *Strongylognathus* species from Tunisia and Italy at seven informative loci. Variants are assigned due to their migratorial velocity towards the anode from slow to fast in the order *e, v, s, m, f, x*, see also Tab. 4, p. 335 in Sanetra *et al.* (1999). n: number of colonies investigated.

Species/Locus	<i>Gpi</i>	<i>G3pdh</i>	<i>Idh</i>	<i>Mdh-1</i>	<i>Pgm-1</i>	<i>Pgm-2</i>	<i>Pk</i>	n
<i>T. biskrense</i> (Tunisia)	<i>e, f, x</i>	<i>s, f</i>	<i>v, m, f</i>	<i>s</i>	<i>e, v, s</i>	<i>m</i>	<i>f</i>	11
<i>T. semilaeve</i> (Tunisia)	<i>v</i>	<i>f</i>	<i>s</i>	<i>s</i>	<i>v, s</i>	<i>m</i>	<i>m</i>	21
<i>T. semilaeve</i> (Italy)	<i>v, f</i>	<i>f</i>	<i>s, f</i>	<i>s</i>	<i>v, s, m</i>	<i>m, f</i>	<i>m</i>	23
<i>S. afer</i> (Tunisia)	<i>f</i>	<i>f</i>	<i>f</i>	<i>s</i>	<i>s</i>	<i>f</i>	<i>s</i>	3
<i>S. destefanii</i> (Italy)	<i>m, f</i>	<i>f</i>	<i>f</i>	<i>s</i>	<i>s</i>	<i>f</i>	<i>s</i>	6

Host species

The *Tetramorium* colonies found infested with *S. afer* contained no sexuals of the host species, as is to be expected for a dulotic social parasite (Buschinger *et al.* 1980). Electrophoretic investigation, however, identified *Tetramorium semilaeve* (for latest attempts to define the species see Sanetra *et al.* 1999, and Cagniant 1997 for North Africa) as the sole host species in the three *S. afer* colonies studied. In non-parasitized host colonies, single queens of *T. semilaeve* were regularly discovered at the time of collection in early spring, hence monogyny can be assumed. A polygynous colony of *T. maurum* Santschi, 1918 was found at Jebel Gora'a in proximity to a *Strongylognathus* colony. This *Tetramorium* species, described from Le Kef, exhibits somewhat enlarged petiolar nodes in females, whilst workers are at present morphologically indistinguishable from *T. semilaeve*. *T. maurum* is also electrophoretically identical to *T. semilaeve* at the loci studied and may constitute a polygynous form of the latter species.

Tetramorium biskrense apparently does not occur in the more northerly part of the range of *S. afer* in Tunisia. However, near Makthar and in the Forêt de Kesra, it was found at the same sites where the slave-maker was detected. Nests of *S. afer* and *T. biskrense* were once found very close (1-2 metres) to one another. However, the suitability of the latter as host species has yet to be seen. The colony structure of *T. biskrense* is at least facultatively polygynous, since five to ten queens (status determined by dissection) were sometimes observed in a nest.

The treatment of the Moroccan *Tetramorium* fauna by Cagniant (1997) as well as results of an excursion to that country by us and others in 1995 revealed a greater species

richness than in Tunisia, with taxa delimitations even more difficult to understand. Based on one or a few workers each investigated morphologically, hosts of the colonies of *S. afer* found in Morocco, as well as those from Algeria (as already cited by Cagniant 1970), can apparently be assigned to a broadly conceived *T. semilaeve*.

Slave raiding behavior

Three successful slave raids were observed in the laboratory, one by each of the three colonies of *S. afer* collected in 1997, of which two were queen-right. These raids were directed towards queen-right host colonies of *Tetramorium semilaeve* from Tunisia. On the other hand, in one experiment with the target colony consisting of *T. caespitum* (Linnaeus, 1758) from Germany, also with its resident queen, the *Strongylognathus* were not able to conquer, though scouting and initial recruitment were observed. Raids lasted for one or two days, usually starting at dusk. Two of the raids began when the ants managed to surmount the partitioning wall during the night despite measures against this, and entered the part of the arena containing the target colony. At the next morning the raid was already in progress. Nevertheless, all constituent elements of typical raiding-behavior (see Buschinger *et al.* 1980) could be documented for *S. afer*.

During the characteristic recruitment on pheromone trails (Sanetra & Buschinger 1996), both *Strongylognathus* and their host workers were engaged in trail running, but the parasites alone seemed responsible for chemical signalling. *Tetramorium* host workers were much involved in combat activities, the intensity of which strongly differed between individual raids. In some cases, *Strongylognathus* workers successfully pierced the head capsules of defending *Tetramorium* with their saber-shaped mandibles. Often, though, the *Strongylognathus* would behave passively towards foreign *Tetramorium*, but almost always survived even vigorous attacks. After recruitment of more nestmates, the *Strongylognathus* displayed peculiar behavioral patterns including quick running, threat with open mandibles and upright posture, obviously intimidating opponents in that way.

After having invaded the target colony, the *Strongylognathus* carried away brood and even adults from the foreign nest. Interestingly, the transportation of adult host workers, a behavior exceptional among slave-making ants, was recorded in high frequency during all slave raids observed in *S. afer*. Group recruitment occurred periodically in waves, alternating with periods of brood and adult transport. The duration of these periods varied from about one to three hours. The two experiments with queen-right *Strongylognathus* colonies resulted in the death of the defeated host colony's queen. Unfortunately, it could not be definitely determined whether the queen was killed by the foreign *Tetramorium* workers or by the slave-makers. In another instance the *T. semilaeve* queen of the raided colony was adopted into the *Strongylognathus* society at the end of a slave raid and survived there for over half a year until culture was discontinued. It should be noted, however, that this *Strongylognathus* colony had been deprived of its resident queen, presumably during collecting.

Discussion

The treatment of *Strongylognathus foreli* as a synonym of *S. afer* is straightforward after the study of almost all existing material of the genus from North Africa. Already Emery (1909) himself had suggested in the first description that var. *foreli* might constitute the worker caste of *S. afer*, then went on to state: "In doubt I consider this variety as new". Female sexuals, which are the most important morph for species distinction in the genus, from four sites in Tunisia and one in western Algeria (holotype of *S. afer*) were nearly identical. In addition, we were unable to decisively correlate any aspect of variation among worker samples with geographic, climatic or habitat variables. Thus, very little doubt remains that only one species of the *S. huberi* group occurs in northern Africa.

It is now desirable to work out the taxonomic relationships of *S. afer* to the similar species of neighboring regions, namely *S. destefanii* Emery, 1915 from southern Italy, *S. insularis* Baroni Urbani, 1968 from Malta and *S. caeciliae* Forel, 1897 from the Iberian Peninsula (see distribution map, Fig. 8). Preliminary investigations showed that structural differences between these four species are weak to non-existent. The female holotype of *S. caeciliae* is no more different from that of *S. afer* than are Tunisian females. However, the worker caste of *S. caeciliae*, though reported (de Haro & Collingwood 1977, Acosta & Martínez 1982, Espadaler 1997), remains undescribed. Its putative description by Baroni Urbani (1969) pertains in fact to *S. huberi* as shown by Sanetra *et al.* (1999). The only obvious difference presently known to us between *S. afer* and *S. destefanii* concerns size, the latter species being somewhat larger on average, with currently no overlap in females. *S. insularis* will doubtlessly prove synonymous to *S. afer* and/or *S. destefanii*. These observations corroborate the general finding that many nominal species of *Strongylognathus* differ no more from each other than different populations or even colonies in most species groups of *Tetramorium* (Bolton 1976). On the other hand, the exuberant degree of morphological variation in workers of the genus *Strongylognathus*, as reported here for *S. afer*, might well be prone to obscure existing differences between species. Hence, further studies on intraspecific variability in *Strongylognathus* will be paramount to establish true species boundaries more convincingly.

One of the most striking features of *S. afer* are the small female sexuals, which barely exceed workers in size. Some eastern Mediterranean and Asian species of the *S. huberi* group have developed similarly minute females. In *S. silvestrii* Menozzi, 1936, known from Greece and Turkey, heads of workers differ in shape from those in *S. afer*, being narrower and more parallel-sided, and the sculpturing is more distinct on average. *S. minutus* Radchenko, 1991 described from Turkmenistan and Uzbekistan is the only *huberi*-group species even smaller than *S. afer*, and the head sides are reported to be not convex at all (Radchenko 1991). Nevertheless, the Asian fauna certainly needs further investigation to assess the significance of these characters.

According to present knowledge, *S. afer* is the only social parasite of *Tetramorium* in North Africa, in contrast to other countries along the coast of the Mediterranean Sea. The

presence in the Maghreb of the inquilines *Strongylognathus testaceus* (Schenck, 1852) and *Anergates atratulus* (Schenck, 1852), widely distributed throughout Eurasia, seems unlikely because their most common host species, *T. caespitum*, appears to be both local and rare. In Morocco, it has obviously been introduced to anthropogenic habitats along the coast and occurs naturally only on mountain tops of the Rif range (Cagniant 1997), while there are no reliable records from Algeria or Tunisia. Other dulotic *Strongylognathus* species are most probably absent from North Africa as well. Thus *S. afer* has been able to penetrate all ecologically suitable habitats without facing competition by other social parasites. Accordingly, the observed distribution pattern of *S. afer* covers a relatively broad altitudinal range, at least from 300 to 1500m, while in other regions of the Mediterranean different slave-making *Strongylognathus* species display preferences to certain types of habitat. For example, in southern Italy, *S. destefanii* has primarily been recorded from coastal areas, while *S. huberi* and *S. alpinus* are confined to more mesic and higher mountainous biotopes, respectively (Sanetra *et al.* 1999). Only once, two of these species were found syntopically.

The area between the Mediterranean Sea and the Sahara desert in Tunisia and north-eastern Algeria ranges from a mediterranean-humid to a mediterranean-arid bioclimate. *S. afer* should be expected to occur more frequently along the coast, where climatic conditions are similar to those favored by its southern European relatives. However, a rather low proportion of records actually originates from that area (see Fig. 7), possibly because of the excessive degradation of habitats in coastal northern Africa. Our new discoveries of *S. afer* in the environs of Makthar are probably located at the southern limit of its distribution, as the tectonically most important mountain ridge of the Tunisian Atlas, which stretches from south-west to north-east, forms a significant climatic transition zone. On its southeastern side, in the lee of the rainy winds, annual precipitation sharply decreases to below 300mm, leading to mediterranean-arid steppe vegetation (Gießner 1964). The present collecting data suggest that these arid environments south of the climatic barrier are not tolerated by *S. afer*. In addition to climatic conditions, the dominance of *Tetramorium biskrense* over the host species *T. semilaeve* in steppe habitats may also be a relevant factor. It is difficult to say if the apparent absence of *S. afer* from less elevated parts of the Medjerda valley and the High Tell is due to the more arid conditions compared with the mountainous parts of that region, or to the excessive use as agricultural land since Punian times. Nonetheless, the change of the natural plant cover alone need not be devastating to *S. afer* and a moderate grazing regime may even have advantageous impacts as the *Tetramorium* hosts are open country inhabitants.

The distribution data hitherto available for *S. afer* show a much lower density of records in Algeria and Morocco than in Tunisia (Fig. 8). Although the Algerian ant fauna has been extensively studied by Cagniant (1968, 1970), the data basis for this large country seems not yet sufficient to assess the abundance of *S. afer* in the extensive central part of its range. Unfortunately, political circumstances in Algeria currently hamper further

research here. The southernmost site in the Saharian Atlas, though geographically isolated, seems ecologically not untypical. Up to recent times there has been a complete lack of *S. afer* records from myrmecologically rather well investigated Morocco, although its presence in the Rif mountains seemed highly likely, owing to records both from western Algeria and, of the very similar *S. caeciliae*, from the Iberian Peninsula. This predictable occurrence in the Rif range has just recently been confirmed (Tinaut in litt.). Surprisingly, one additional record of *S. afer* from far south in the High Atlas has become available (Cagniant 1997), but it remains the only colony found by H. Cagniant during his 17 years of collecting in Morocco (Cagniant in litt.). The apparent rarity of *S. afer* in Morocco has also been corroborated by our excursion in 1995, when intensive searching in the High and Middle Atlas mountains failed to turn up *Strongylognathus*. We cannot presently explain why *S. afer* might be less common in Morocco than in Tunisia, since suitable habitats in a reasonable state of conservation, even with dense *T. semilaeve* (s.l.) populations are frequent in many mountainous areas of Morocco. The systematics of the rather rich Moroccan *Tetramorium* fauna is still barely understood (Cagniant 1997). Thus, a lower abundance of ordinary monogynous *T. semilaeve* suitable as hosts might be one possible explanation, as we often observed polygynous colonies.

The host workers reported in this study and by Forel (1890b) belong to *Tetramorium semilaeve*, in a broadly defined sense. Forel (1890b) additionally cited *T. punicum* (Smith, 1861) as the host of *S. afer*, but that name should be treated as a *nomen dubium* (Sanetra *et al.* 1999). A dark color form of *T. semilaeve* is the best explanation for Forel's observation. *T. maurum* (doubtfully distinct from *T. semilaeve*, see results) and *T. biskrense* were never positively identified as slave species of *S. afer*, though the latter was frequently found nesting in close vicinity to *Strongylognathus* colonies at the more southern localities. This apparent restriction to a single host species probably results from the common occurrence of multiple queens in *T. maurum* and *T. biskrense*, which might render colony foundation difficult for this slave-maker. However, the exact mode of colony founding remains unknown in *Strongylognathus*. Founding queens in some dulotic ant species are adept in killing or driving off more than one host queen (e.g., Buschinger *et al.* 1980), but the use of polygynous slave species has not been recorded in *Strongylognathus* so far. It seems nevertheless conceivable that polygynous *Tetramorium* species or populations serve as additional hosts, whose workers are occasionally enslaved during raids but which may be unsuitable for colony foundation.

Most other nominal *Tetramorium* taxa reported from Tunisia are probably based on local populations of *T. semilaeve* (*jugurtha* Menozzi, 1934, *atlante* Cagniant, 1970) or *T. biskrense* (*kahenae* Menozzi, 1934, *jarbas* Cagniant, 1970, both synonymized with *T. biskrense* by Cagniant 1997). There is evidence that three more valid *Tetramorium* species inhabit Tunisia, none of which, however, can be regarded as a potential host of *S. afer*. Firstly, *T. juba* Collingwood, 1985, a distinct species described from the Algerian Sahara, appears to occur in arid environments in southern Tunisia (sample from Nefta, Gouv.

Tozeur, coll. A. Schulz; tentatively identified). The two other species, which clearly show Afrotropical affinities (see Bolton 1980), are *T. sericeiventre* Emery, 1877, recorded from southern Tunisia by Santschi (1918), and *T. exasperatum* Emery, 1891. The latter was found once during the 1997 excursion (7 rkm N Ghardimaou, ca. 600m, 12.IV.1997, leg. M. Sanetra), close to its type locality at Ain Draham in the coastal range of northern Tunisia. It is related to the Afrotropical *T. simillimum* (Smith, 1851) species group rather than to other Palearctic *Tetramorium*.

Observations by Forel (1890b) that the parasites are more frequent in the nests and larger than their hosts let him suggest dulotic life habits for *S. afer*, which, however, had not been confirmed until now. The slave raiding behavior recorded in this study does not apparently differ from the usual pattern observed in other dulotic *Strongylognathus* species of the *S. huberi* group (Kutter 1920, 1923, Sanetra & Buschinger 1996, unpubl.). However, the peculiar trait of enslaving adult host workers, termed eudulosis by Kutter (1957), is markedly developed in *S. afer*, while *S. destefanii* exhibited this behavior only sporadically in laboratory experiments. Raiding adult workers is extremely uncommon in other dulotic ant genera (Buschinger *et al.* 1980), having but rarely been observed in *Polyergus rufescens* (Latreille, 1798) by Le Moli *et al.* (1994). It is not yet understood by what means the *Strongylognathus* actually overwhelm foreign host colonies. It seems that mechanisms other than mandible fight, such as ritualized dominance behavior and/or the use of chemical weapons, are valuable elements in finally defeating the raided colonies. Host queen incorporation by orphaned *Strongylognathus* societies, also a surprising observation, has occasionally been recorded in other species in laboratory experiments (Sanetra & Buschinger 1996).

The discovery of a sole dealate female in early October near Makthar indicates the season of swarming at that time, at least in the southern mountainous part of the range. It may occur somewhat earlier in the eumediterranean lowlands. In comparison to their *Tetramorium* hosts and also *S. testaceus*, development of sexuals in the Mediterranean species of the *S. huberi* group is delayed, with a presumed swarming period not before the middle of September to the beginning of October (Sanetra unpubl.). Though much remains to be elucidated, with the findings added here to the previously scanty literature information, *Strongylognathus afer* can now be regarded as one of the best investigated species of the genus.

Acknowledgements

We wish to pay sincere thanks to Alberto Tinaut (Granada), Andreas Schulz and Kathrin Vock (Leichlingen) who allowed us to use their unpublished records of *Strongylognathus afer*. Andreas also made useful suggestions for the descriptions and, above all, graciously prepared the drawings. A. Tinaut, Henri Cagniant (Toulouse) and Xavier Espadaler (Barcelona) most kindly sent us Moroccan and Algerian *Strongylognathus* samples for study

and provided habitat information. Valter Raineri and Roberto Poggi (Genova), Bernhard Merz (Genève), Michel Brancucci (Basel), Piero Baronio (Bologna) and Manfred Koch (Berlin) provided important material from public collections. Lutz Lelgemann (Darmstadt) participated in allozyme studies of Tunisian *Tetramorium* and *Strongylognathus* samples as well as in observations of slave raids during a practical course. Maps were prepared using DMAP for Windows by Alan Morton (Windsor). Lynn Atkinson kindly improved the English. This study was in part supported by a grant by the Deutsche Forschungsgemeinschaft (DFG) to Alfred Buschinger (Darmstadt) (Bu 310/26-1).

References

- Acosta, F.J. & Martínez, M.D. (1982) Consideraciones sobre la dulosis en el género *Strongylognathus* Mayr, 1853. (Hym. Formicidae). *Boletín de la Asociación Española de Entomología*, 6, 121-124.
- Baroni Urbani, C. (1969) Gli *Strongylognathus* del gruppo *huberi* nell'Europa occidentale: saggio di una revisione basata sulla casta operaia (Hymenoptera Formicidae). *Bollettino de la Società Entomologica Italiana*, 99-101, 132-168.
- Bolton, B. (1976) The ant tribe Tetramoriini (Hymenoptera: Formicidae). Constituent genera, review of smaller genera and revision of *Triglyphothrix* Forel. *Bulletin of the British Museum of Natural History (Entomology)*, 34, 281-379.
- Bolton, B. (1980) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. *Bulletin of the British Museum of Natural History (Entomology)*, 40, 193-384.
- Bolton, B. (1995) *A new general catalogue of the ants of the world*, Harvard University Press, Cambridge (Mass.), 504 pp.
- Buschinger, A., Erhardt, W. & Winter, U. (1980) The organization of slave raids in dulotic ants - a comparative study (Hymenoptera; Formicidae). *Zeitschrift für Tierpsychologie*, 53, 245-264.
- Cagniant, H. (1968) Liste préliminaire de fourmis forestières d'Algérie. Résultats obtenus de 1963 a 1966. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 104, 138-147.
- Cagniant, H. (1970) Deuxième liste de fourmis d'Algérie récoltées principalement en forêt (1^{re} partie). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 105[1969], 405-430.
- Cagniant, H. (1997) Le genre *Tetramorium* au Maroc (Hymenoptera: Formicidae): clé et catalogue des espèces. *Annales de la Société entomologique de France (Nouvelle série)*, 33, 89-100.
- de Haro, A. & Collingwood, C.A. (1977) Prospeccion mirmecologica por Andalucía. *Boletín de la Estacion Central de Ecología*, 6(12), 85-90.
- Espadaler, X. (1997) Catàleg de les Formigues (Hymenoptera: Formicidae) dels Països Catalans. *In: IX Sessió Conjunta d'Entomologia, Institució Catalana d'Història Natural – Societat Catalana de Lepidopterologia, Barcelona 1995*, Barcelona, 23-42.
- Emery, C. (1884) Materiali per lo studio della fauna Tunisina raccolti da G. e L. Doria. III. Rassegna delle formiche della Tunisia. *Annali del Museo Civico di Storia Naturale di Genova*, series (2)1[=21], 373-386.
- Emery, C. (1909) Beiträge zur Monographie der Formiciden des paläarktischen Faunengebietes. (Hym.). Teil IX. *Deutsche Entomologische Zeitschrift*, 1909, 695-712.
- Forel, A. (1890a) Fourmis de Tunisie et d'Algérie orientale. *Bulletin ou Comptes-rendus des Séances de la Société entomologique de Belgique*, 34, 61-76.

- Forel, A. (1890b) Eine myrmekologische Ferienreise nach Tunesien und Ostalgerien nebst einer Beobachtung des Herrn Gleadow in Indien über *Aenictus*. *Humboldt*, 9, 296-306.
- Gießner, K. (1964) *Naturgeographische Landschaftsanalyse der tunesischen Dorsale (Gebirgsrücken)*. Jahrbuch der Geographischen Gesellschaft Hannover, 1964, Hannover.
- Gießner, K. (1984) Naturraum und landschaftsökologische Probleme. In: Schliephake, K. (Ed.). *Tunesien. Geographie-Geschichte-Kultur-Religion-Staat-Gesellschaft-Bildungswesen-Politik-Wirtschaft*, Thienemann, Stuttgart, 23-74.
- Kutter, H. (1920) *Strongylognathus Huberi* For. r. *alpinus* Wh. eine Sklaven raubende Ameise. *Biologisches Zentralblatt*, 40, 528-538.
- Kutter, H. (1923) Der Sklavenräuber *Strongylognathus huberi* For. ssp. *alpinus* Wheeler. *Revue Suisse de Zoologie*, 30, 387-426.
- Kutter, H. (1957) Eine neue Form der Sklavengewinnung bei Ameisen. *Umschau*, 1957, 327-329.
- Le Moli, F., Mori, A. & Grasso, D.A. (1994) Behavioural ecology of the obligatory slave-making ant, *Polyergus rufescens* Latr. (Hymenoptera, Formicidae). *Memorabilia Zoologica*, 48, 133-146.
- Pisarski, B. (1966) Etude sur les fourmis du genre *Strongylognathus* Mayr (Hym.: Formicidae). *Annales Zoologici (Warszawa)*, 23, 509-523.
- Radchenko, A.G. (1991) Ants of the Genus *Strongylognathus* (Hymenoptera, Formicidae) of the USSR. [In Russ.]. *Zoologicheskii zhurnal*, 70(10), 84-90. [Translation: *Entomological Review*, 71(2) (1992), 40-48.]
- Sanetra, M. & Buschinger, A. (1996) Slave raiding behaviour in socially parasitic *Strongylognathus* ants (Hymenoptera: Formicidae). In: *Proceedings of the XX International Congress of Entomology, Firenze, 1996*, Firenze, 399.
- Sanetra, M. & Buschinger, A. (2000) Phylogenetic relationships among social parasites and their hosts in the ant tribe Tetramoriini (Hymenoptera: Formicidae). *European Journal of Entomology*, 97, 95-117.
- Sanetra, M., Heinze, J. & Buschinger, A. (1994) Enzyme polymorphism in the ant genus *Tetramorium* Mayr and its social parasites (Hymenoptera: Formicidae). *Biochemical Systematics and Ecology*, 22, 753-759.
- Sanetra, M., Güsten, R. & Schulz, A. (1999) Taxonomy and distribution of Italian *Tetramorium* species and their social parasites. *Memorie de la Società Entomologica Italiana*, 77, 317-357.
- Santschi, F. (1918) Nouveaux *Tetramorium* africains. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 9, 121-132.
- Seifert, B. (1996) *Ameisen beobachten, bestimmen*, NaturBuch-Verlag, Augsburg, 352 pp.
- Stille, M. (1996) Queen/worker thorax volume ratios and nest-founding strategies in ants. *Oecologia*, 105, 87-93.